Ecological Characteristics of the New York State Butterfly Fauna (Lepidoptera)

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Abstract: "Niche breadth" as reflected by occurrence in nine ecological regions of New York State is examined by family for the 142 species of butterflies recorded in the state fauna. Species/genus ratios are also examined by families and regions. Data on voltinism and immigration are presented. It is concluded that "niche breadth" is smallest in the Lycaenidae and Hesperiidae and that the ecological distribution of species in these families in the regions with the largest faunas (excluding immigrants) tends to increase the species/genus ratio.

INTRODUCTION

New York State is one of the best-collected and most thoroughly documented areas for butterflies in the United States. The fauna has recently been reviewed in detail (Shapiro, in press). A total of 142 species has been recorded for the state. This is a sufficiently large fauna for ecologically significant information to be extracted from its composition and distribution.

ECOGEOGRAPHIC DISTRIBUTION AND "NICHE BREADTH"

The ecological geography of New York is complex. Thompson (1966) presents various regional classifications of the state based on climate, landforms, vegetation, etc. A convenient summation of these only partially concordant classifications is the division of the state into nine ecogeographic regions based broadly on physiography (Shapiro, in press) (Fig. 1). Each region includes a variety of habitats; relative areas of the regions may be estimated from the figure. The occurrence of each butterfly species in each region has been tabulated (presented in full in Shapiro, *ibid.*). The number of regions in which a species occurs may be taken as a crude index of its "niche breadth," at least insofar as its New York range is concerned. Table 1 gives the occurrence by number of regions of species grouped into five major "families" (sens. lat.). Separate tabulations are given with and without species which occur in New York only as immigrants; these have a significant impact on the overall pattern. The sources and seasonal characteristics of immigration into New York are discussed in Shapiro (*ibid.*).

These data are not strictly comparable with previously published distributions

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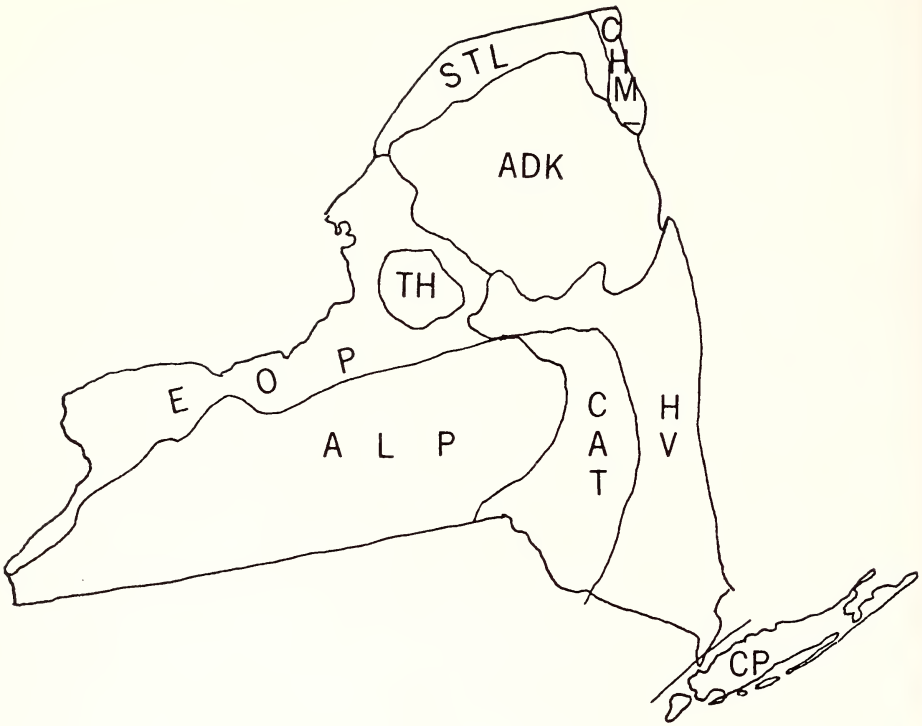

FIG. 1. Ecogeographic regions of New York. Abbreviations: CP, Coastal Plain; HV, Hudson Valley; CAT, Catskill Mts.; ALP, Allegheny Plateau; ADK, Adirondack Mts.; TH, Tug Hill Plateau; EOP, Erie-Ontario Plain; STL, St. Lawrence Valley; CHM, Champlain Valley.

of "niche breadth," based on measurements such as occurrence by habitat types (several examples in Williams, 1964). Such distributions typically give a more-or-less U-shaped graph when number of species is plotted against the measure of breadth. The New York data give a trimodal plot reminiscent of that derived by Williams (1964) from the data of Emmel and Emmel (1962) on the butterfly fauna of Donner Pass, California. There, "niche breadth" is based on occurrence in ten habitats of four general types.

Table 1 also includes the mean number of regions/species on a family-by-family basis. Comparison of the tables with and without immigrants demonstrates the role of these species in lowering the average "niche breadth" of species in the families with especially large numbers of immigrants. In the resident fauna, the Lycaenidae and Hesperiidae appear to have especially narrow niches.

In Table 2, the characteristics of the regional faunas are examined in terms of "niche breadth" of the component species (as expressed by number of regions

Table 1*a*. Number of species in each butterfly family occurring in different numbers of ecogeographic regions in New York, including immigrant species.

Family	Number of regions									Total # of species	Mean # of regions/ species	% of species found in all 9 regions
	1	2	3	4	5	6	7	8	9			
Nymphalidae	6	1	0	6	5	3	1	3	15	40	5.0	37.5
Lycaenidae	6	1	4	3	4	1	3	2	5	29	4.8	17.1
Pieridae	3	4	1	1	2	0	0	0	3	14	3.9	21.4
Papilionidae	1	0	0	2	2	0	0	0	2	7	5.3	28.6
Hesperiidae	9	6	5	8	8	4	2	1	9	52	4.5	19.2
Total # of species:	25	12	10	20	21	8	6	6	34	142	4.9	24.0

of occurrence and by voltinism) and the role of immigration both from outside the state and from outside the region (including out-of-state). Of all of these bases, the Coastal Plain has the most distinctive fauna. This single region, moreover, contributes sixteen species not found in any other region and has the largest fauna of any region, with 83.8 percent of the total New York fauna although it has an area comparable to Tug Hill, with only half as many species in a very severe climate.

Tables 3 and 4 demonstrate the degree of faunal relationship among all possible pairs of regions. In Table 4, this is quantified as the percentage of each given regional fauna shared with each of the others, and also the percentage of each other regional fauna found in it. A more complex matrix showing the consistency of co-occurrence of species in regions has also been prepared. Very similar patterns are obtained when various suggested formulae for faunal affinity (Long, 1963) are substituted for these simple percentages. Such formulae attempt to combine the two components of faunal resemblance given in Table 4.

On a regional basis species distributions must be interpreted as a continuum rather than as a set of discrete associations, but a strong tendency toward as-

Table 1*b*. Same, excluding immigrant species.

Family	Number of regions									Total # of species	Mean # of regions/ species	% of species found in all 9 regions
	1	2	3	4	5	6	7	8	9			
Nymphalidae	3	1	0	4	5	3	1	3	13	33	6.4	39.4
Lycaenidae	4	1	4	3	4	1	3	2	5	27	5.1	18.9
Pieridae	0	2	1	1	1	0	0	0	3	8	5.4	37.5
Papilionidae	0	0	0	2	2	0	0	0	2	6	6.0	33.3
Hesperiidae	3	5	3	8	8	4	2	1	9	43	5.1	20.9
Total # of species:	10	9	8	18	20	8	6	6	32	117	5.6	27.4

TABLE 2. Ecological characteristics of the regional faunas. Regional abbreviations are as in Figure 1.

	Region								
	CP	HV	CAT	ALP	ADK	TH	EOP	STL	CHM
Total species recorded	119	106	81	107	57	46	94	52	48
% recorded from $\geqslant 5$ regions in N.Y.	56.2%	68.0	90.1	71.0	89.9	73.9	77.7	90.4	100%
% recorded from $\leqslant 2$ regions in N.Y.	22.7%	7.5	1.2	3.7	5.3	4.3	4.3	4.0	0%
% immigrant from out-of-state	18.9%	8.5	3.7	9.3	3.5	4.3	9.6	4.0	4.1%
% immigrant from out-of-region (includes out-of-state)	24.4%	12.3	6.2	15.0	3.5	6.5	11.7	7.5	4.1%
% univoltine	38.9%	44.3	55.5	57.0	60.0	63.0	56.4	60.0	60.4%

sociations could be expected on a habitat basis. The Coastal Plain and Hudson Valley can be considered "southern" regions and Tug Hill and the Adirondacks "northern," with intergradation through the others, especially the Allegheny Plateau and Erie-Ontario Plain. The peak in the 4 to 5 region range reflects this; both "northern" and "southern" species are able to occupy that many regions, but a sixth carries either one too far into unfavorable environment for successful occupation to occur.

SPECIES-TO-GENUS RATIOS

The ratio of the number of species to number of genera in a fauna or flora has been taken as a measure of intrageneric competition by various writers, but its interpretation has been inconsistent and often controversial (cf. Williams, 1964; Elton, 1946). The New York data are of special interest since species-to-genus ratios can be obtained not only for the entire state but for the regions

TABLE 3. Number of species shared by pairs of regions in New York.

Region	CP	HV	CAT	ALP	ADK	TH	EOP	STL	CHM
CP	(119)	98	67	94	45	39	84	45	44
HV		(106)	74	99	44	39	87	47	47
CAT			(81)	81	53	44	74	48	47
ALP				(107)	49	44	80	49	48
ADK					(57)	44	48	45	43
TH						(46)	41	39	36
EOP							(94)	48	47
STL								(52)	42
CHM									(48)

Table 4. Relationships of the regional faunas. Above the diagonal: Percentage of the fauna in the diagonal recorded in each other fauna (read across the columns to the right). Below the diagonal: Percentage of each other fauna recorded in the fauna in the diagonal (read down the rows from the diagonal).

Region	CP	HV	CAT	ALP	ADK	TH	EOP	STL	CHM
CP	(100)	82.4	56.3	79.0	37.8	32.8	70.6	37.8	37.0
HV	92.4	(100)	70.0	93.4	42.5	37.0	82.1	44.3	44.3
CAT	82.7	91.3	(100)	100.0	65.4	54.3	91.3	59.3	58.0
ALP	90.3	92.5	75.7	(100)	45.8	41.1	74.7	45.8	44.9
ADK	78.9	77.2	93.0	86.0	(100)	77.2	84.2	78.9	75.4
TH	85.0	85.0	95.7	95.7	95.7	(100)	89.1	84.8	78.2
EOP	89.8	92.5	78.7	85.1	51.1	43.6	(100)	51.6	50.0
STL	86.5	90.4	92.3	94.0	86.5	75.0	92.3	(100)	80.7
CHM	91.7	97.9	97.9	100.0	89.5	75.8	97.9	87.5	(100)

and thus can be related to the overall faunal richness and its environmental component. The butterfly fauna of New York corresponds well to a logarithmic series (Table 5), suggesting that its classification is internally reasonably consistent and can also be compared with other faunas. Table 6 gives the regional and total species-to-genus ratios with and without immigrants. There is a broad correlation of large faunas with larger numbers of species per genus. This correlation is partly obscured where large numbers of immigrant species are included, since most of them are the only representatives of their genera in the fauna. These data suggest in a very general sense that more congeners can coexist in areas with milder climates, i.e., that finer subdivision of the environment into minimally competitive niches can be achieved. This statement agrees with most current ecological thought.

In Table 1 there was a strong suggestion that "niche breadth" is different in the butterfly families, and when species-to-genus ratios are examined on a per-family basis they support this inference. In Table 7, the number of genera

Table 5. Genera and species in the New York fauna and their fit to a logarithmic series.

Species/genus	Observed	Number of species calculated from log series
1	39	38.3
2	14	13.4
3	4	8.9
4	6	6.7
5	5 ($\sum_{1}^{5} = 68.0$)	5.4 ($\sum_{1}^{5} = 72.7$)
6	1	4.5
7	0	3.8
8	1	3.4
	70	84.4

Total: 142 species in 70 genera.

TABLE 6. Species/genus ratios of the New York regional faunas.

Region	Including immigrants			Excluding immigrants		
	Total # of species	Total genera	Species/ genus	Total # of species	Total genera	Species/ genus
CP	119	63	1.90	97	48	2.02
HV	106	55	1.93	98	48	2.04
CAT	81	39	2.08	78	37	2.11
ALP	107	54	2.00	98	47	2.09
ADK	57	31	1.84	55	30	1.83
TH	46	28	1.67	44	27	1.62
EOP	94	48	1.96	86	42	2.05
STL	52	32	1.62	50	31	1.61
CHM	48	29	1.66	46	28	1.70
	142	70	2.03	117	54	2.18

containing one to eight species is given on a family basis. In the New York fauna, the Lycaenidae and especially the Hesperiidae have many monotypic genera. On the other hand, only two genera have more than five species, and these are both Hesperiidae-*Polites*, with six (one immigrant), and *Erynnis*, with eight (seven sympatric on the Coastal Plain); and the Lycaenids have two of seventeen genera with more than three species (*Satyrium, Incisalia*) and the Hesperiids five of 25 (*Erynnis, Hesperia, Polites, Poanes, Euphyes*), accounting for more than half of the thirteen such genera (out of 70). Also, congeners in the Lycaenidae and Hesperiidae tend to be sympatric while those in Nymphalidae and Pieridae tend to replace one another geographically.

The role played by the Hesperiidae in the New York fauna, of a large, dominant family (52 of 142 species, 36.7 percent) of specialized species, corresponds to that of the Lycaenidae in the Sierra Nevada (28 of 74 species, 37.8 percent at Donner Pass, Emmel and Emmel, 1962; 49 of 134 species, 36.5 percent, Yosemite, Garth and Tilden, 1963), and to the Plebeiinae and Satyrinae in various Palaearctic faunas. The roles of the Lycaenidae and Hesperiidae are effectively reversed in New York and at Donner Pass: New York Lycaenidae number 29 (20.4 percent) and Donner Pass Hesperiidae ten (13.5 percent). The

TABLE 7. Number of genera with one to eight species, by families, in the New York fauna.

Family	Number of species							
	1	2	3	4	5	6	7	8
Nymphalidae	8	5	3	2	1	0	0	0
Lycaenidae	12	2	1	0	2	0	0	0
Papilionidae	2	0	0	0	1	0	0	0
Pieridae	2	2	0	2	0	0	0	0
Hesperiidae	15	5	0	2	1	1	0	1
Total:	39	14	4	6	5	1	0	1

Table 8. Number of species per family and region in the New York fauna.

Family	Region								
	CP	HV	CAT	ALP	ADK	TH	EOP	STL	CHM
Nymphalidae	31	31	29	33	26	20	31	20	21
Lycaenidae	23	31	17	23	12	7	17	10	10
Papilionidae	7	6	4	6	2	2	6	2	2
Pieridae	10	7	5	8	5	4	8	6	3
Hesperiidae	48	41	26	37	12	13	32	14	12
Total:	119	106	81	107	57	46	94	52	48

role of the Nymphalidae in the two localities is the same (New York, 40/142, 28.2 percent; Donner Pass, 23/74, 31.1 percent).

Table 8 gives the number of species per family in each region. As might be expected, the numbers of Hesperiidae and Lycaenidae drop rapidly in the regions with small faunas, while the number of Nymphalidae remains high and the relative importance of the family increases in the smaller regional faunas. Note in Table 1 that both the mean number of regions occupied/species and the percentage of all species found in all nine regions are highest in this family, also indicating broad adaptation.

HOST SPECIALIZATION

One measure of "niche breadth" not yet mentioned is specialization to the larval host plant. Data on this point are only partial. Ideally, the hosts for each species should be recorded in each region. In practice, each species has been classified into one of three categories on the basis of its recorded hosts state wide. No records not actually from New York have been considered. The categories are: "monophagous," recorded on only one plant genus; "oligophagous," recorded on two or more genera in the same plant family; and "polyphagous," recorded on two or more plant families. This classification, based on plant taxonomy, pays no attention to the chemistry of host-insect relationships, although in those cases where it is known it seems to control host selection, and although it often cuts across wide taxonomic boundaries. The chemistry of host selection is understood only for three or four New York butterflies.

In Table 9, these data are presented on a regional basis for all species for which satisfactory host data are available. Overall, oligophagy is the commonest condition, but in the regions with the largest faunas monophagy is nearly as frequent or more so, indicating a high incidence of specialization. In the regions with small faunas, the relative dominance of oligophagy increases. There is little increase in polyphagy, which occurs in few species in New York state (these are nearly all of very wide distribution).

Most specialization patterns are not dramatically different among the butter-

TABLE 9. Distribution of monophagy (M), oligophagy (O), and polyphagy (P) by families and species in each region.

Region	Family	M	O	P	Region	Family	M	O	P
CP	Nymph.	10	10	6	ALP	Nymph.	11	11	6
	Lycaen.	11	6	3		Lycaen.	10	6	4
	Pap.	2	1	3		Pap.	2	1	3
	Pier.	2	5	0		Pier.	3	4	0
	Hesp.	17	16	2		Hesp.	12	15	2
	Total:	42	38	14		Total:	38	37	15
	%:	44.4	41.7	14.9		%:	42.2	41.1	16.7
HV	Nymph.	9	11	6	ADK	Nymph.	9	9	3
	Lycaen.	9	6	4		Lycaen.	6	2	2
	Pap.	2	1	3		Pap.	0	1	1
	Pier.	2	5	0		Pier.	1	4	0
	Hesp.	13	16	2		Hesp.	1	6	1
	Total:	35	39	15		Total:	17	22	7
	%:	39.3	43.9	16.8		%:	37.0	47.8	15.2
CAT	Nymph.	9	11	5	TH	Nymph.	8	7	3
	Lycaen.	6	5	3		Lycaen.	4	1	2
	Pap.	0	1	3		Pap.	0	1	1
	Pier.	2	3	0		Pier.	1	3	0
	Hesp.	6	12	1		Hesp.	1	7	1
	Total:	23	32	12		Total	14	19	7
	%:	34.3	47.7	18.0		%:	35.0	47.5	17.5
EOP	Nymph.	10	11	6	STL	Nymph.	7	9	3
	Lycaen.	7	5	3		Lycaen.	8	1	2
	Pap.	2	1	3		Pap.	0	1	1
	Pier.	2	4	0		Pier.	2	4	0
	Hesp.	8	14	2		Hesp.	0	9	1
	Total:	29	35	14		Total:	17	24	7
	%:	37.2	44.8	18.0		%:	35.4	49.9	14.7
CHM	Nymph.	9	10	3	State-wide	Nymph.	11	11	6
	Lycaen.	5	2	2		Lycaen.	12	6	4
	Pap.	0	1	1		Pap.	2	1	3
	Pier.	0	3	0		Pier.	4	6	0
	Hesp.	0	8	1		Hesp.	18	17	2
	Total:	14	22	7		Total:	47	41	15
	%:	32.5	51.2	16.3		%:	45.6	39.8	14.6

fly families in New York. The Nymphalidae have a surprisingly large number of monophagous species, but most of these feed on widespread and common plant genera. The small Papilionid and Pierid faunas are consistent across the state. In the Lycaenidae and Hesperiidae, oligophagy often involves several alternate or seasonal hosts, none of which is especially common or widespread. Indeed, the narrowness of some butterfly niches may be defined by the low probability of finding two or more required host species close together.

CONCLUSION

One of the central problems of community ecology is the nature of the factors determining species diversity. Interspecific competition is one of these factors, acting in ecological time through competitive exclusion and in evolutionary time through character displacement. The data on New York State butterflies support the familiar gradients of species richness associated with latitude and climate, and, at the same time, they suggest strongly that the adaptive responses of different families to these conditions have produced different patterns of resource allocation and niche differentiation.

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